17. Mendelian Experiments on Fowls.

By J. T. Cunningham, M.A., F.Z.S.

[Received October 25, 1911: Read February 6, 1912.]

I. Experiment 1.—*Bankiva* ♂ × *Silky* ♀.

Crosses between Silky fowls and other breeds have frequently been tried, both before and since the formulation of the Mendelian doctrine. The silky character of the feathers has always been found to be recessive, and this was noticed before the recently awakened interest in Mendel's theory. Thus Tegetmeier (1867, p. 224) found that the F_1 hybrids of Silkies with other breeds had normal plumage, and Darwin (1876, chap. vii.) noted the same result in the offspring of a white Silky hen mated to a Spanish cock.

Bateson (1909, pp. 34, 35, 181) mentions the heredity of the comb, of the silky character, and of the pigmentation of the skin, describing experiments on the latter character in detail. He also discusses (ibid. p. 103) the heredity of the white colour of the Silky. Bateson's results and conclusions will be discussed in reference to the results of the experiment here recorded. C. B. Davenport (1906, p. 55) describes a cross between Silkies and Frizzled fowls, but he reared only the direct offspring of the cross, the F_1 generation.

My experiment was made with a pair of F_1's kindly given to me by Mr. D. Seth-Smith. These had been reared in the Society's Gardens from a cross between a male of the Jungle Fowl (*Gallus bankiva*) and Silky hens, and my attention was called to the interest of this cross by Mr. Frank Finn, F.Z.S. The Jungle cock may not have been perfectly pure bred, but there is no evidence that its pedigree was impure. The characters of these original parents are as follows:—

Jungle Fowl ♂.
  Comb, single.
  Colour of plumage, black-red: breast and tail-feathers black, neck and saddle hackles yellowish red.
  Skin, unpigmented: comb and wattles red.
  Legs, clean, not feathered.
  Feet, normal, four toes on each.
  No crest on head.

Silky Fowl ♀.
  Comb, small, rose.
  Colour of plumage, white.
  Skin, black; comb and wattles black-red, ear-lobes blue.
  Legs, feathered.
  Feet, with double hallux on both.
  Crest of feathers on head behind comb.

Thus, including the silky character of the feathers, contrasted with the normal, we have seven pairs of characters the heredity of which is to be investigated.

In the F_1 specimens the following characters are dominant :—

Coloured plumage.
Normal structure of plumage.
Rose comb.
Black pigmentation of skin.
Double hallux.
Feathering of legs.
Crest on head.

But the dominance is somewhat irregular. Thus, one hen of F_1 at the Gardens had a single comb. Several of the F_1's had a normal foot on one side and a double hallux on the other. The majority had the double hallux on both sides. In my pair the cock has both feet normal and the hen has both feet abnormal, with double hallux. This irregularity of dominance of the extra toe has been noticed by previous experimenters. The crest is dominant, but much smaller in the F_1's than in the Silky. The skin in my pair is pigmented, but not so dark as in the Silky; it looks blue instead of black. The feathered leg is dominant, the feathering being present in all the F_1's but the feathering is less than in the Silky. These facts on the whole agree with the idea of dominance as the presence of a positive character (presence and absence theory of dominant and recessive), which in the F_1 is present only in one half of the zygote, *i. e.*, in one of the gametes which are united in the cross, and therefore naturally does not produce so much effect as when it is carried by both gametes. Thus the crest, the feathering of the legs, and the pigmentation of the skin may be said to be intermediate in F_1 between the conditions in the two parents. The dominance, however, seems sometimes to fail, as in the case of the specimen with a single comb, and the specimens with double hallux on one foot only or on neither. The failure of dominance of the rose comb is not mentioned by Bateson, who states that the dominance of the rose comb is very definite and that it is generally quite impossible to distinguish pure rose from the heterozygous type containing single. On the other hand, exceptions to the dominance of the extra toe are common, and are mentioned by Bateson, who states that it occurs in all cases yet studied in birds and mammals.

In all F_1 specimens the coloured plumage and the normal structure of the feathers are present; these characters are completely dominant.

In other crosses which have been described in the experiments above referred to much greater irregularity of dominance has been observed. Thus Bateson found, with regard to the pigmentation of the skin, that when the Silky hen was crossed with a Brown Leghorn cock all the F_1 offspring, both male and female, were either destitute of pigmentation or showed only a small amount of it in certain parts. But when the opposite cross was made, Silky cock with Brown Leghorn hen, the F_1 males had unpigmented skins, while the females were almost as much pigmented as the pure Silky hens. Bateson explains these results by the assumption that there are three pairs of characters or allelomorphs affecting the results, namely :—

Presence and absence of femaleness.
Presence and absence of the black pigmentation.
Presence and absence of a factor which can suppress or mask the development of the pigmentation.

He assumes that this last factor is double or homozygous in the Brown Leghorn cock, single or heterozygous in the Brown Leghorn hen, and absent in the Silky. There is no need for such assumptions in the case of the Bankiva cock, but it must be noted that I have no experience of the opposite cross, Bankiva hen with Silky cock.

In the experiment here considered the white colour of the Silky plumage is perfectly recessive. This result also differs somewhat from that of previous experiments. Davenport crossed a Silky cock with Frizzled hens, but he states that the colour of Frizzles is not constant but variable. His hens were of various colours—dark brown, yellowish, light brown, and mixed black yellow and red. Some of them may have been carrying white as a recessive. Of his F_1 hybrids 7 were white and 25 coloured. Davenport considers that the results do not agree with either the hypothesis that white is recessive or that it is dominant. He concludes that the white is not always dominant, but this seems to be a slip: he probably means that the colour is not always recessive.

Bateson found that the white of the Silky, though recessive to colour, gave coloured offspring when crossed with certain other recessive whites obtained from crossings. He concludes, therefore, that the whiteness of the Silky is due to the absence of one of two elements which together produce colour. We shall have to consider this point again in discussing the colours of the F_2's which form the point of chief interest in my results.

We now come to the consideration of the F_2 generation, that is of the chicks which I have hatched and reared from the pair of F_1's above mentioned. The first brood was hatched on May 15th, 1911, and consisted of nine chicks, one of which died within the first few days; the other eight are still alive and vigorous. The hen afterwards sat again, but this time hatched only two chicks, probably in consequence of the very dry weather; these two were hatched in August. The following table (p. 244) shows the characters of these chickens.

The numbers of these specimens are, of course, too small to afford evidence of any importance with regard to the numerical proportions in which the characters or combinations of characters

Cross Silky ♀ × *Bankiva* ♂.

F_2 generation.

	Colour of Plumage.	*Structure of Plumage.*	*Comb.*	*Pigmentation of Skin.*	*Toes.*	*Feathering of Legs.*	*Crest.*
1. ♂.	White.	Normal.	Rose.	Black.	Normal.	Much feathered.	None.
2. ♂.	White.	Silky.	Rose.	Normal.	Double hallux on both feet.	Moderately feathered.	Slight.
3. ♂.	Coloured.	Silky.	Rose.	Black.	Normal.	Moderately feathered.	Crest.
4. ♂.	Coloured.	Normal.	Rose.	Normal.	Normal.	Moderately feathered.	Crest.
5. ♂.	Coloured.	Normal.	Single.	Black.	Normal.	A trace of feathering.	Slight.
6. ♀.	Coloured.	Normal.	Single.	Black.	Normal.	Moderately feathered.	Crest.
7. ♀.	Coloured.	Normal.	Rose.	Black.	Normal.	Moderately feathered.	None.
8. ♀.	Coloured.	Normal.	Single.	Black.	Normal.	Moderately feathered.	Crest.
Second Brood.							
9. ♀.	White.	Normal.	Rose.	Black.	Normal.	Feathered.	Crest.
10. ♂.	White.	Silky.	Rose.	Normal.	Normal.	Quite clean.	Crest.

occur, and it is not the object of this paper to draw conclusions as to factors or segregation from the numerical proportions. It is assumed that characters united in F_1 tend to segregate in F_2, and that the explanation of this segregation is the separation in the gametes of F_1 of the pairs of factors, so that half the gametes contain one character and the other half its allelomorph, as it is called. My object here is merely to draw attention to certain points in my results which indicate that the segregation is not necessarily complete. If we consider single characters and take only the eight chicks of the first brood, omitting the one that died, and the two of the second brood, we see that the Mendelian proportion of 3 dominants to 1 recessive is, in many of the characters, either exactly or approximately exhibited. Thus we have in the colour of the plumage 6 coloured to 2 white, in the structure of the feathers 6 normal to 2 silky, in the combs 5 rose to 3 single, in the colour of the skin 6 black to 2 normal, in the crest 6 with crest to 2 without. The double hallux, however, occurs only once, instead of six times, and as the male F_1 had normal feet although the extra toe character was present in the cross, it is by no means certain that this character was segregated in his gametes. The feathering of the legs and the crest on the head exhibit a condition which does not harmonise exactly with the Mendelian theory. The leg-feathering is present in all the specimens except No. 10 in the second brood, but it exhibits very different *degrees* of development. One explanation of this may be that such a character is naturally more developed in the dominant homozygote, where the character was present in both gametes, than in the heterozygote, where it was present only in one, and this is probably the case. But there is one specimen, No. 5, in which the feathering is the merest trace, and Mendelism affords no explanation of such variations within a character, it merely takes account of its presence or absence. Similar remarks may be made concerning the crest: of the 8 chicks of the first brood there are 6 with crest and 2 without, the Mendelian proportion, and there are 4 with well-developed crest and 2 with a very slight crest. The latter may be the heterozygotes for this character, although there should be four of these to two dominant homozygotes.

I have noticed an interesting correlation between the crest and the character of the comb. As Bateson points out, the rose comb of the Silky has its posterior end divided into three irregular points. He describes the comb as a rose plus a trifid element which is the cause of this condition of the posterior end, and states that in F_2 from Silky × Single, regular rose combs are produced in those individuals which have the rose factor without this trifid element. In other words, the comb of the Silky is represented not by one factor but by two. The regular or ordinary rose comb, as it occurs in Hamburg fowls, has a flat upper surface which is triangular in shape, the apex of the triangle, called the peak or pike, being free from the head and projecting backwards. Bateson's statements are for the most part confirmed by my results, but I have a somewhat different interpretation to offer. The rose comb of the Silky is not only trifid posteriorly but abbreviated. This character occurs in both the F_1's in my experiment; it is dominant. In the F_2's the same character occurs in all those that have a crest, both males and females, although the comb is much smaller in the hens. The two specimens without a crest, on the other hand, No. 1 ♂ and No. 7 ♀, have the normal rose comb with a projecting point behind. The crest makes no difference to the shape of the single comb. There is thus a correlation between the crest of feathers and the truncated trifid character of the rose comb: these two characters either occur together or are absent together. I believe, however, that this is not a coupling of two distinct characters but that they are both manifestations of one character. What Bateson calls a trifid element is in my opinion nothing but the crest; the factor which causes the development of the crest of the feathers also causes the posterior truncation of the comb.

The most remarkable and interesting result in my experiment is the condition of the recessive whites in the first brood of F_2's. Both of these whites show some colour, while according to the Mendelian theory of segregation they ought to show none. The specimen No. 1, now (Sept. 30, 1911) 4½ months old and in mature plumage, has a band of colour across the back behind the shoulder; when I first noticed this colour it was a very pale yellowish tinge, so slight that it was difficult to be sure that it was actually pigment in the feathers and not accidental staining. Now it is darker and more orange, and there is also a slight yellow tinge in the neck hackles. The other white, No. 2, has also some slight colouring, a faintly tinted region on the back like the other, and some very pale patches on the neck ventrally and over the eye on each side. These white specimens were yellowish white in the down when first hatched, but this is no evidence of colour, for the down of the chicks of white fowls, as of white ducks, is always yellowish. The two whites of the second brood do not yet show any colour.

Now this fact shows that the Mendelian doctrine of complete segregation and gametic purity is not always true. The fact that these recessive whites do appear in the F_2 generation shows clearly that gametic segregation does take place in the F_1 individuals, but in my experiment the recessive white is not exactly the same as the original white of the Silky: it is no longer pure, but is mixed with a little of the colour factor with which it has been mixed in F_1. We must consider whether the result obtained by me is explained in any degree by Bateson's conclusion concerning the white of the Silky. As already mentioned, he concludes that this white is due not to the absence of all colour factors, but to the absence of one out of two which together produce colour. Now this partial colour factor cannot explain my result, for it cannot by itself produce any colour, and the essential point of the Mendelian doctrine is that the recessive individual in F_2 is homozygous, *i. e.* due to the union of two gametes each of which carries the factor for the recessive character. The recessive character in the case under consideration is the white of the Silky, and the white in the individuals of F_2 which I have described is not the same as the white of the original Silky. Bateson states that the adult Silky is pure white as a rule, but the down of the chickens has some colour usually though perhaps not always. The colour in this case is buff, not blue or black, and it occurs on the sides of the head and on the rump. This again has nothing to do with the result I have described, for the colour in my F_2 whites was not observed in the chicks, or in the mature plumage when first developed, but appeared later, and gradually increased in intensity. I have not examined pure Silky chicks, as I have not reared any.

It is, I think, certain that in this particular case the recessive character derived from a cross is not pure, and this naturally suggests that no recessives derived from crosses are perfectly pure. The determinants of these characters in the hybrid individuals have been mixed in the F_1 individuals with the determinants of other characters. Whatever the determinants may be, whether special chemical compounds such as ferments, or parts of chromosomes, it is possible that the mixing in F_1 is such that each determinant is affected, tainted as it were by the other. If this were the case it would tend to throw doubt on the whole conception of species and varieties reared on the Mendelian phenomena. It may be that segregation occurs not because the determinants or factors in the gametes are indivisible units, but because the determinants of certain pairs of characters are too different to mix completely, while others less different would show more mixture. In any case the recessive white in my experiment is not pure, and it is improbable that it is the only case of its kind. I hope next season to breed from these whites and study the heredity of the colour character in the F_3 generation.

Prof. Punnett, in conversation with me on this subject, made two different suggestions in explanation of the colour in the white recessive. The first was that the Silky is not a perfectly white breed, but normally carries a little yellow colour, which is usually present in the cocks but not in the hens. As the stock of Silkies from which my cross came were all hens, and I have no experience of Silky cocks, I cannot disprove this suggestion, but can only point out that it does not agree with the account of Silkies given by Davenport, nor with that given in Wright's 'Book of Poultry,' which says the plumage should be pure white. The second suggestion was that the yellow or yellow to red colour of the Bankiva might be a distinct factor from that of the black pigment, and therefore be segregated independently. This seems to me an untenable hypothesis, as, if it were true, we ought to get wholly black and wholly yellow or red birds in F_2, and no such cases have occurred. Moreover, the F_2 bird No. 1 in my experiment has produced one or two single feathers on the back which contain black pigment as well as yellow. I have plucked out one such feather and preserved it.

EXPERIMENT 2.—*Japanese Long-tail* ♂ × *Dorking* ♀.

The second experiment I have to describe was chronologically the earlier, but is less complete and less important than that already described. It consisted in crossing a Japanese Long-tailed cock with a Dorking hen. Crosses between the Long-tailed fowls and other breeds have been previously made by C. B. Davenport at the Carnegie Station for Experimental Evolution at Cold Spring Harbour, New York, U.S.A. ('Inheritance in Poultry,' Washington, 1906). In his first experiment Davenport crossed a cock of the Long-tailed breed, which he refers to by its proper Japanese name of Tosa fowl, with a White Cochin Bantam hen. Six F_1's were reared, 3 cocks and 3 hens. The males were all of the male Tosa-fowl coloration except that every feather was repeatedly barred with white. The females were all of the female Tosa-fowl coloration except that the light shafting was very much broadened. The female Tosa in this case is described as "black mossed with rusty with a straw-coloured shaft to each feather." All three males developed abnormally long middle tail-feathers, in other words the tail character of the Tosa was dominant.

Of the F_2 generation 57 individuals were hatched: of these 16 were white and 41 pigmented, which approximates to the theoretical proportion of one in four. But of the 16 whites only 5 were without trace of reddish pigment, which occurred on the breast, top of head, and remiges. Davenport draws from this the same conclusion that I have suggested in the case of my cross between Silky and Jungle fowl, namely that segregation is not always perfect, and the gametes from which these whites arose were not pure for the white character. As the F_2's were immature at the time of publication, the inheritance of the long-tailed character in this generation could not be described.

With regard to the F_1's, Davenport points out that the two sexes, except for the admixture of the white colour, resemble the male and female Tosa fowl respectively, and remarks that from a germ-cell of the male Tosa either a bird coloured like a male Tosa or one coloured like a female Tosa may arise, that the male germ-cells contain the Anlagen not only of the male characteristic but also of the female characteristic. The same result is equally evident in the results of my cross between the male Jungle fowl and the White Silky, the hens in F_1 and the coloured ones in F_2 showing the coloration and markings of the female Jungle fowl. This conclusion is in opposition to the Mendelian view that the female is heterozygous but the male homozygous, the latter not carrying the female character. Mendelians argue that the effects of castration in male vertebrates generally can be explained as merely the non-appearance of male characters, and they would probably maintain that the coloration of the hens referred to in these cases was merely the absence of the male characters. But it is necessary to distinguish between somatic or secondary characters and the actual sex. It is certain that the somatic characters of the female of a particular breed are actually transmitted by the male, and there are no facts known which support the assumption that positive characters, if the female possessed them, would not be transmitted in the same way.

In a second experiment Davenport crossed the Tosa male with a female dark Brahma. In this case only the F_1 generation was reared, namely 16 males and 5 females. In some of the male hybrids the tail-feathers showed greater length than those of the adult Brahma, but as they were only six months old at the time the Report was written, the inheritance of the tail character was not completely known.

In my cross between the Tosa cock and Dorking hen only three F_1 chicks were hatched and reared in 1905. They were all hens. Two of them had the double hallux which occurs in the Dorking, on both sides, the third on one side only. The combs were larger than those of the Japanese hens; the coloration was speckled much like that of the Japanese hens, each feather with a light shaft, but the coloration of the Dorking hen is not very different, and I did not pay much attention to this character.

In 1906 the three F_1 hens were kept with a pure-bred Japanese cock. The eggs of the hybrids were brown in shell-colour, while those of the old Dorking hen were white. The egg-colour of the Japanese was therefore dominant. This is another case for the Mendelians to consider. Surely the colour of the egg-shell must be a female character, and here it is transferred to the female hybrids by the male. The eggs were also smaller than those of the Dorking, another egg character derived from the Japanese cock.

Two broods of F_2's, *i. e.* F_1 ♀ × Jap. ♂, were reared. In the first brood 5 chicks were hatched and 3 died in the egg: two of the 5 had the double hallux, three had normal toes, all those in the egg had normal toes. Thus the number with double hallux was 2 out of 8, whereas the expectation, as the character is dominant, was equal numbers of each character. Ultimately three of these chicks were reared, and all were cocks, one with double hallux, two with normal toes.

The second brood hatched consisted of 11 chicks, of which 3 had the double hallux and 8 had normal toes. The two broods together therefore give 5 with double hallux to 14 with normal toes, where the expectation was equal numbers. Of the second brood 5 were cocks and 6 hens. Thus of the F_2's there were in all 8 cocks, and if the long tail was dominant every one would show it, while if it were recessive half would have the long tail and half the short tail of the Dorking. The result showed that the character was dominant, as it was recognised in all the birds except one which died before the character was definitely visible.

One cock and five hens of these F_2's were kept to breed from, all of them with normal toes, all those with the extra toe having been killed off. From these were hatched and reared in 1907 5 F_3's (2 cocks and 3 hens), and in 1908 8 F_4's (3 cocks and 5 hens). In all these cocks the Japanese character of the tail was observed, although they were not all kept long enough to develop any great length of feathers. The result, however, is not conclusive with regard to segregation or absence of segregation in the tail character, for the F_2 cock bred from F_1 ♀ and Japanese ♂ might itself have been a pure dominant in this character, in which case all the F_3's would have been either homozygous or heterozygous dominants. Similarly, the F_3 ♂ kept for breeding might have been a homozygous dominant, and segregation would then not be evident in F_4. A complete experiment to test the segregation of the Japanese Long-tail character is therefore yet to be made.

The double hallux did not reappear in any of the F_3 or F_4 generations, which supports the view that the normal toe in the F_2's is a pure recessive.

II. *Incomplete Segregation of the Pigmentation of the Silky Fowl.*

In Part I. of this paper, when describing the characters of the F_2 generation from a cross between Bankiva male and Silky female, I treated the inheritance of the peculiar pigmentation of the Silky as a case of simple segregation. When I wrote that part, I had only examined the F_2 birds in the living condition, in which there is a conspicuous contrast between the sooty colour of the combs and wattles in the majority and the blood-red colour of the others which seemed obviously recessives. Afterwards it occurred to me that if there were incomplete segregation in the colour of the plumage the recessives in other characters also might be impure. I was led to consider the possibility of slight degrees of body pigmentation by the description of such degrees given by Bateson and Punnett in their recent paper in the 'Journal of Genetics,' vol. i. no. 3. Accordingly I killed No. 10 of the F_2's, which had the white colour and silky character in its plumage, and apparently normal colour in comb and skin, that is to say the comb etc. was blood-red, and the skin, so far as could be seen between the feathers, unpigmented. Before the bird was plucked, however, I noticed a ring of dark colour on the lips of the cloacal aperture. On further examination I found considerable pigmentation of the subcutaneous tissue of the abdomen behind the sternum, which was the cause of the darkening, above mentioned, of the lips of the cloaca. There was subcutaneous pigment on the tarsal joint and all down the tarsometatarsus, but none on the knee-joint. It occurred also on the elbow-joint of the wing and on the wrist-joint, but not at the shoulder-joint. In all these cases the pigment was visible externally as a darkening of the skin, and under the microscope as a reticulum of pigment cells in the connective tissue. On the peritoneum the pigmentation was slight but distinct, not only on the outer wall but also over the intestines, for example over the gizzard; the surface of the testes was also black over the anterior three fourths of the organs, while the posterior fourth was white.

The next thing to be done was to make a thorough examination of a normal specimen of *Gallus bankiva* in order to compare it with the recessive just described. Fortunately, the cock of the original cross being now rather old and blind of one eye, was available for the purpose and was placed at my disposal and killed and plucked. I found a little pigment in the subcutaneous tissue about the ankle-joint posteriorly, but none in the periosteum: this pigment was merely a slight extension of the pigment on the inner surface of the skin, which extended down the tarso-metatarsus as in the F_2 recessive. In both cases the shanks appeared externally olive-green. In the Bankiva there was no pigmentation anywhere else, either in the subcutaneous tissue of the abdomen or of the wing-joints, nor in the peritoneum, and the surface of the testes was white.

It is certain, then, that the pigmentation present in the F_2 recessive is not derived from the Bankiva, but must have come from the Silky, with the exception of that of the shanks, which occurs in both breeds. The next question is whether the recessives are all pigmented to a similar degree or whether some are destitute of pigmentation. Of such recessives, as seen in the list given in Part I. of this paper, there are three. One of these, No. 2 of the first brood, is still alive, being kept for breeding; so far as can be seen it is in the same condition as the one which was killed, as it shows the dark colour round the cloaca. The third, No. 4 of the first brood, also a male, was killed before I thought of looking for slight degrees of pigmentation, and therefore I can say nothing about it. In any case, we have the fact that one of the recessives is not pure, and therefore segregation is not complete and perfect in the gametes, as the Mendelian theory assumes. It may perhaps be suggested that slightly pigmented F_2's are not recessives at all but heterozygotes, but this in the ordinary sense is impossible, because such birds do not occur in F_1, in which all are heterozygotes. The only possible conclusion is that there is a tendency to segregation, but that the recessive character when it separates is no longer pure but is, at any rate in some individuals, modified by a slight degree of the opposite character; or if we adopt the presence and absence theory, we may say that the positive character is not entirely absent from the recessive individuals, but that distinct traces of it are present in them.

It is necessary now to make a detailed comparison between my experiment and those described by Bateson and Punnett in the paper to which reference has already been made. It will be seen that the inheritance of the pigmentation of the Silky in different crosses is exceedingly curious and complicated. Bateson and Punnett crossed the Silky with specimens of a certain strain of Brown Leghorns in their possession. When the Silky hen was mated with the Brown Leghorn cock, the F_1 chicks, instead of being strongly pigmented as in the experiment I have described, were scarcely pigmented at all. It appears at first sight as if in the Silky × Bankiva cross the pigmentation is dominant, while in the Silky-Leghorn the same character is recessive. Many of the F_1 chicks were reared, and in the adult state were almost indistinguishable in general appearance from pure unpigmented birds. Thus these F_1 birds were in appearance similar to the F_2 recessives described by me, though in constitution they were very different. I shall have to return to this point later. Careful examination of the F_1's in Bateson and Punnett's experiment showed traces of pigmentation. These are described as sometimes patches on the wattles, skin, or shank; pigment was also often found in the periosteum of the femoro-tibial or tarso-metatarsal joints and frequently in the peritoneum. No mention is, however, made of pigmentation under the skin of the abdomen or on the wing-joints as in my F_2 recessives.

On the other hand, when the reciprocal cross was made, namely Silky cock with Brown Leghorn hen, the results were markedly different: the males were like those of the first cross, but the females were all deeply pigmented. It might be said that in this case the pigmentation was dominant in the females, recessive in the males, while when the Brown Leghorn was the male parent the pigmentation was recessive in both sexes. It is certainly remarkable to meet with such a sexual difference as this in a character which showed no signs before the crosses were made of being in any way sexual. No such sexual difference in the F_1's has been found to occur in the cross with which I have experimented, or in crosses with the Silky described by other naturalists. In all other crosses known the F_1's were deeply pigmented; and Bateson and Punnett point out that the almost complete absence of pigmentation in one or both sexes of the F_1's in their case is related to the fact that the Brown Leghorns used by them had unpigmented shanks, while most breeds normally have pigment in the skin of the shanks, as in the *Gallus bankiva* described above.

Bateson and Punnett explain their results as due to the segregation of three pairs of hypothetical factors, namely, P, p, presence and absence of pigmentation, I, i, presence and absence of a factor which inhibits the development of the pigmentation, and F, f, presence and absence of femaleness. It may be noted here as an instance of the difficulty of keeping pace with Mendelian theories, that Bateson seems to have already abandoned his former theory of sex according to which maleness and femaleness were alternative to each other, for he now suggests that there may be another pair of characters, presence and absence of maleness. The inhibition factor I is supposed to be homozygous in the male Brown Leghorn, heterozygous in the female, and the pigmentation factor to be homozygous in both sexes in the Silky. With regard to sex a further assumption is made, namely, that when an individual is heterozygous for both F and I, these two in segregation cannot pass into the same gamete, as there is a repulsion between them. The female, moreover, is considered to be always heterozygous for femaleness, while the male is homozygous for the absence of this factor. All these factors being assumed, whether any real meaning can be attached to them or not, their segregation according to the Mendelian theory is shown to produce results which agree approximately with those observed. But the approximation is not very close, there are many serious discrepancies between the expected and the actual results.

The next point to be considered is the nature of the inhibition factor in the Brown Leghorn. We have seen that the difference between this breed and others, such as *Gallus bankiva*, with regard to pigmentation, is that in the latter the skin of the shanks is pigmented, while in the Leghorn they are unpigmented. The difference, then, is in the degree of pigmentation. Why should the less degree of pigmentation be called an inhibition factor? It may be said it does not much matter what term is used so long as we agree as to the facts. But there is more here than a mere difference of terms. Bateson and Punnett assume that the inhibition factor forms a pair of factors segregating independently of the pigmentation factor and its absence. I see no justification for this. It seems more probable that the unpigmented character is alternative or allelomorphic to the pigmented, and in F_1 is dominant in the case of the Brown Leghorn because it is of a higher degree than in breeds with pigmented shanks. It is interesting to note that in Reptiles, which represent the ancestors of Birds, pigmentation in the skin and internal connective tissue is of general occurrence. It would seem, then, that in birds generally the pigment was transferred to the feathers and disappeared from the skin and interior of the body, but remained in the skin of the shanks, which is still, excepting those few species and breeds which have feathered legs, in the reptilian condition covered with epidermic scales. In the Brown Leghorn fowl this last remnant of the internal pigmentation has disappeared. But there is no evidence of a distinct factor inhibiting the development of pigment. There is no more reason for assuming the existence of such a factor in a bird with unpigmented shanks than in one in which the shanks, but not the rest of the body, are pigmented. In the latter case Bateson and Punnett admit that the unpigmented condition is recessive to the pigmentation of the Silky, and it is obviously more reasonable and more scientific to regard the condition of the Brown Leghorn as merely a higher degree of the unpigmented character. Such a higher degree would naturally imply that there is a stronger hereditary tendency in the Brown Leghorn to the absence of pigmentation, and therefore it is not surprising that this character should be dominant in the cross with the Silky. It seems to me, then, more probable that the unpigmented character in Bateson and Punnett's experiments is directly alternative or allelomorphic to the pigmented; and I shall endeavour to show that their results can be as well, if not better, explained on this hypothesis as on their own. It will be evident from this paper that I am far from denying the occurrence of segregation, which is an obvious fact, although my own results show that it is not necessarily absolute or complete. It is further evident that a sexual difference could not appear in the F_1's if there were not already some sexual difference in one or both of the two breeds crossed. The pigmentation tends to appear in the female sex more than in the male: this not only occurs in the F_1's of the cross Silky ♂ × Brown Leghorn ♀, but a similar tendency is seen, according to Bateson and Punnett, in the shanks of other breeds. It is not, then, an unreasonable hypothesis that the female Brown Leghorn has a greater tendency to the development of pigmentation, or that the hereditary tendency towards the unpigmented character is weaker in this sex and therefore not dominant. We may also assume that when fertilisation takes place, whether we regard femaleness as segregated from maleness or each of them as alternatively dominant, the tendency to pigmentation accompanies the female character. To express these assumptions in Mendelian fashion, we may write W for the unpigmented character which is dominant, and Wp for the weaker unpigmented character, retaining P for the pigmentation of the Silky. Then, instead of the complicated formulæ of Bateson and Punnett we should have the two reciprocal crosses expressed as follows:—

(A.) Brown Leghorn ♂ × Silky ♀.
WW ♂ PP ♀.
Gametes W + W P ♂ + P ♀.
F_1 ......WP ♂ + WP ♀.

(B.) Silky ♂ × Brown Leghorn ♀.
PP ♂ WWp ♀.
Gametes P + P W ♂ + Wp ♀.
F_1 ......WP ♂ + Wp P ♀.

The above formulæ are not to be taken as implying that sex is determined entirely by the female, or that either sex does not contain the other in a latent condition, but merely that, as half the ova in fertilisation must actually give rise to females, the tendency to pigmentation passes only into these females.

We have next to see how this works out for the F_2's. According to Bateson and Punnett's formulæ, the F_2's from cross A are for the males 6 slightly pigmented to 2 unpigmented, for the females 3 slightly pigmented, 3 fully pigmented, and 2 unpigmented. According to my hypothesis the results would be as follows:—

F_1......... WP ♂ × WP ♀.
Gametes W + P W + P.
F_2......... WW + 2WP + PP.

That is 1 unpigmented, 2 slightly pigmented, and 1 fully pigmented in both males and females.

Bateson and Punnett point out that according to their formulæ no fully pigmented males would be expected from this mating, while as a matter of fact a considerable proportion of fully pigmented males actually occurred, namely 12 out of a total number of 75. They regard these as of the constitution ffPPII or ffPPIi, and suppose that in the presence of a double dose of the pigmentation factor the effects of the inhibitor are in considerable measure overcome, in corroboration of which view they found that these specimens became less fully pigmented when adult. But here they have made a mistake in reading their own formulæ, for the combination PP occurs only once among the males (namely ffPPIi, fig. 4, p. 190 of the paper), and therefore the expectation on their own interpretation would be 1 in 8, not 1 in 4 as they assume. The actual numbers are:—

	Males.			Females.		
	Full.	*Some.*	*None.*	*Full.*	*Some.*	*None.*
	12	42	21	28	28	13
Correct expectation acc. to B. & P.	9·4	46·8	18·75	26	26	17
Expectation acc. to my hypothesis.	18·75	37·5	18·75	17·25	34·5	17·25

It will be seen that the numbers obtained by experiment of fully pigmented males are too large for Bateson and Punnett's hypothesis and too small for mine, while it must be admitted that the numbers of females agree more closely with their assumptions than with mine. If we add together the numbers for the two sexes we have:—

Full.	*Some.*	*None.*
40	70	34,

which is a close approximation to the expectation on my hypothesis,

36	72	36.

The differences, therefore, between the actual results and the expectation on my hypothesis are an excess of fully pigmented females and of partially pigmented and unpigmented males, with a deficiency of fully pigmented males. These differences would be explained if segregation were, as I have shown it to be in my experiment, incomplete, and at the same time pigmentation tended to develop more in the females. Thus in the females the WW's would be partially contaminated by P, and some of them would be partially pigmented instead of unpigmented, while some of the WP's would appear as fully pigmented instead of partially so. In the males, on the other hand, the PP's would be affected by W, and this would reduce the number of fully pigmented in that sex and increase the number of partially pigmented.

We have now to consider the F_2 generation from the mating B in which the Silky is the male and the Brown Leghorn the female. According to the formula of Bateson and Punnett the expectation is 3 fully pigmented, 3 partially pigmented, and 2 unpigmented in each sex. This expectation is fairly well fulfilled in the males, but in the females there is a great excess of fully pigmented over the partially pigmented: the former are nearly half as many again as the latter, and this the authors call a slight excess. The complete numbers are:—

	Males.			Females.		
	Full.	*Some.*	*None.*	*Full.*	*Some.*	*None.*
	56	55	34	74	55	38
Expectation	52·5	52·5	35	62·5	62·5	42

According to my hypothesis the F_1's are

WP ♂, Wp P ♀,

and the gametes

W + P, Wp + P.

The zygotes therefore will be

W Wp, W P, Wp P, P P.

The first and last of these are the same as those which occurred in the original parents, while the second and third are the zygotes of the male and female F_1's. This is the ordinary result of Mendelian segregation in the F_2: one pure dominant, one pure recessive, and two heterozygotes. The difficulty is to decide what will be the distribution of the sexes among these zygotes. If we suppose that Wp is always coupled with the female character, then all the W Wp's and Wp P's will be females, and all the rest males. But this would make not only the W P's but also all the P P's male, and it seems improbable that the pure Silky character in the F_2 should be confined to one sex. We may conclude that the P P's will be of both sexes and likewise the W Wp's. We may assume that the heterozygotes W P and Wp P will be in the same condition as in the F_1, the former all males, the latter all females. Thus we shall have for the males

W Wp, 2 W P, P P,

and for the females

W Wp, 2 Wp P, P P.

In the males, therefore, the ratio should be one unpigmented, two partially pigmented, and one fully pigmented. It must be admitted that this does not agree with the actual results obtained by Bateson and Punnett; but if segregation is not always complete, some of the W P's might appear in F_2 as fully pigmented and would then be added to the P P's, and the number of partially pigmented and fully pigmented might be equal.

In the females on my hypothesis there should be one unpigmented to three fully pigmented, and none partially pigmented. This again does not agree with the actual figures; but if segregation is incomplete, the P in the Wp P may be affected by the W, and so a certain number of females might appear as partially pigmented. In any case there is actually a great excess of fully pigmented females over the partially pigmented, whereas according to Bateson and Punnett the numbers should be equal.

There is another point in Bateson and Punnett's figures of the F_2's from this cross which may be of great importance, although it is not noticed by the authors themselves. According to their hypothesis the total numbers of the sexes should be equal, whereas they are actually 140 males to 167 females. Thus there is not only an excess of fully pigmented females over the partially pigmented, but a large excess, more than 19 per cent., of females over males. This excess occurs in almost every family, and it seems improbable that it should be accidental. In the F_2's from the reciprocal cross Leghorn ♂ × Silky ♀, on the other hand, there is an excess of males, 75 to 69 females. It would appear that the Leghorn was not only dominant as to character, but prepotent as to sex. I cannot attempt to explain this, but it is not in accordance with Mendelian theory.

In any case we are justified in saying that the actual results obtained by Bateson and Punnett in the F_2 generation do not agree in either of the reciprocal crosses with their assumptions, and that there is nothing in their results to prove that imperfect segregation may not occur in the cross of Silky with Brown Leghorn. It would scarcely be profitable to compare in detail the results of all the other matings recorded by Bateson and Punnett with those which would be expected on my hypothesis; the comparisons would be similar to those already given as examples. It is sufficient to point out that all their explanations are founded on the assumption that the pigmentation of the Silky is inherited as an indivisible unit, and that the result of my experiment shows that this assumption is contrary to fact.

In view of the subdivision of the pigmentation character proved by my results, the remarks of Bateson and Punnett on p. 201 of their paper are somewhat curious. They state that the F_1 birds, either of both sexes or of the male sex only, according to the mating, in respect of the intensity of their pigmentation might belong to either of their three classes, slight, some, or moderate, and that their experience has been that these classes grade very much into one another. Further on they remark that it would be possible to choose birds of the F_2 generation from Silky ♀ × Brown Leghorn ♂, and to arrange them in a series exhibiting continuous gradation from full pigmentation to none at all. "Yet we now know," they assert, "that such a series is due to the interaction of three definite factors, inclusive of the sex factor, and that the continuity of variation manifested is in reality founded upon a discontinuous basis." It seems to me that this is a misuse of words: we know nothing of the kind. What we know is the continuous gradation; and even apart from the results of my experiment, the discontinuous basis to which the authors refer is purely hypothetical. Moreover, one cannot help asking, in the light of the above quoted remarks, what value is to be attached to the distinction of the three degrees of pigmentation, full, some, and none, on the numbers placed under which degrees the validity of the factors assumed by the authors entirely depends.

In view of the failure of complete segregation in the two characters dealt with in this and the preceding paper, it is natural to consider whether any of the other characters present in the two forms crossed also fail to segregate. This point is more difficult to decide in the other characters. There could be no doubt that the white plumage and the unpigmented skin were recessive with a trace of the dominant character, but in other characters any condition short of complete absence might possibly belong to the heterozygote.

The double hallux. This character obviously does not behave in the normal Mendelian fashion. In F_1 the double hallux is dominant but not completely so: in my F_1 cock both feet were normal, in the hen both feet had the double hallux. In F_2 there are nine normals to one with double hallux, but no intermediates.

Feathering of legs. There appear in the F_2's to be two homozygous dominants, six heterozygous, and two recessives. If this is the correct interpretation, one of the recessives contained a trace of the dominant character, the degree of feathering being infinitesimal, only a few very minute feathers between the large scales. I am inclined to think that the only specimen recorded as having quite clean legs had really a trace of the character, for although no actual feathers were visible, the lower edges of the scales showed a slight ridge.

Crest. There are two specimens, Nos. 1 and 7, one cock and one hen, with no trace of crest and the rose comb pointed behind. These seem to be pure recessives showing complete segregation.

But there are also two, Nos. 2 and 5, in which the crest is very slight, less than in the F_1. No decided conclusions can be drawn in this case.

Comb. I have not yet observed any intermediates between rose comb and single.

Silky Plumage. I have not yet observed incomplete segregation in this character.

Many cases in which the results of crossing experiments are not completely in accordance with the Mendelian theory are mentioned by Bateson in his 'Mendel's Principles of Heredity' (1909), among them being the double hallux, the leg-feathering, and the crest of fowls.

In the light of the facts which I have recorded, the doctrine known as Mendelism cannot be said to be based on sufficient evidence to justify the notorious dogmatism of its supporters. Mendelians assume that heredity is the transmission of unit characters, which may sometimes combine to form a new character which is transmitted as a whole, but that the units cannot be subdivided. If subdivision occurs it is assumed to be due to the fact that a supposed unit was really compound; if, however, the process of segregation is at least in some cases not complete, but each character after a cross is mingled with some fraction of the opposite character, the assumption of units and all that is founded upon it falls to the ground. It is possible that segregation is only incomplete between characters which differ from one another in degree and not in kind, for example between pigmentation and absence of pigmentation in fowls. But if the doctrine now generally adopted by Mendelians of presence and absence is valid, it is difficult to see how this difference could exist. Hitherto, Mendelian experiments have been too exclusively carried out on the assumption of indivisible characters, whether real or imaginary, and the object kept in view has been to find, or invent, factors whose complete segregation would agree with the observed results. There is a promising field for research in the investigation of the divisibility of real characters.

References.

TEGETMEIER, W. B.—1867. The Poultry Book. London: Routledge.

DARWIN, C.—1876. Variation of Animals and Plants under Domestication. 2nd Edition, Vols. I. & II.

BATESON, W.—1909. Mendel's Principles of Heredity. Cambridge University Press.

DAVENPORT, C. B.—1906. Inheritance in Poultry. Publications of the Carnegie Institution of Washington, No. 52. Papers of Station for Experimental Evolution, No. 7.

BATESON, W., & PUNNETT, R. C.—1911. The Inheritance of the peculiar Pigmentation of the Silky Fowl. 'Journal of Genetics,' Vol. I. No. 3, p. 185.